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Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales

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Given that soaring birds travel faster with supportive winds or in good thermal soaring conditions, we expect weather conditions en route of migration to explain commonly observed regional and seasonal patterns in the performance of soaring migrants. We used GPS-loggers to track 13 honey buzzards and four Montagu's harriers for two to six migrations each. We determined how tailwinds, crosswinds, boundary layer height (a proxy for thermal convection) and precipitation affected hourly speeds, daily distances and daily mean speeds with linear regression models. Honey buzzards mostly travel by soaring while Montagu's harriers supplement soaring with flapping. Therefore, we expect that performance of harriers will be less affected by weather than for buzzards. Weather conditions explained between 30 and 50% of variation in migration performance of both species. Tailwind had the largest effect on hourly speeds, daily mean speeds and daily travel distances. Honey buzzards travelled significantly faster and farther, and Montagu's harriers non-significantly faster, under better convective conditions. Honey buzzards travelled at slower speeds and shorter distances in crosswinds, whereas harriers maintained high speeds in crosswinds. Weather conditions varied between regions and seasons, and this variation accounted for nearly all regional and seasonal variation in flight performance. Hourly performance was higher than predicted at times when we suspect birds had switched to intermittent or continuous flapping flight, for example during sea-crossings. The daily travel distance of Montagu's harriers was determined to a significant extent by their daily travel time, which differed between regions, possibly also due to weather conditions. We conclude with the implications of our work for studies on migration phenology and we suggest an important role for high-resolution telemetry in understanding migratory behavior across entire migratory journeys.

Migrating birds encounter widely varying weather conditions throughout their seasonal journeys. Weather conditions may affect the timing of migration onset (Shamoun-Baranes et al. 2006), stop-over schedules (Drake 2007, Bauer et al. 2008, Arizaga et al. 2011, Ma et al. 2011), the route followed by migrants (Bohrer et al. 2012), and their speed during travel (Gordo 2007, Shamoun-Baranes et al. 2010). If adverse weather conditions are met during migration, birds risk delayed arrival and poor body condition, which in turn may affect their competitiveness or reproductive success (Drake et al. 2014). Thus, weather influences during migration may carry over to later stages of the annual cycle (McNamara et al. 1998, Smith and Moore 2005, Newton 2006, Norris

and Marra 2007). Unfortunately, despite that the travel speeds of many migratory organisms clearly depend on the environmental conditions through which they travel (Luschi et al. 2003, Stefanescu et al. 2007, Tøttrup et al. 2008, 2012), it is not clear yet if weather affects migrating birds differently between different stages of their migration cycle (Shamoun-Baranes et al. 2010, Gordo et al. 2013). However, for large birds, we are now able to record flight behavior as well as the weather conditions which they encounter over entire migratory journeys, due to recent advances in animal tracking and meteorological modeling.

The way weather affects migration depends on the flight mode of a bird, which is largely determined by its body size and morphology (Alerstam 1990, Hedenström 1993, Pennycuik 2003, 2008, Shamoun-Baranes et al. 2010). Storks, pelicans and raptors tend to soar on thermals and orographic updrafts to avoid the high energetic cost of flapping flight (Hedenström 1993). Consequently, the migratory itineraries of obligate soaring migrants are limited

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by the availability of suitable soaring conditions en route (Shamoun-Baranes et al. 2010). For example, strict soaring migrants do not usually travel at night when thermal updrafts are absent and tend to circumvent large bodies of water where such updrafts are too weak to support soaring (Kerlinger 1989, Bildstein 2006). Soaring birds may also interrupt their travel under adverse weather conditions (Thorup et al. 2006) which may cause delays in their annual schedules (Allen et al. 1996, Leshem and YomTov 1996a, Shamoun-Baranes et al. 2006). Moreover, soaring birds achieve higher ground speeds under stronger updraft conditions (Bruderer et al. 1994, Spaar and Bruderer 1996, 1997a), and they choose local flight paths along landscape features that support strong updrafts (Leshem and YomTov 1996a, b, Maransky et al. 1997, Alpert et al. 2000, Brandes and Ombalski 2004). The ground speed of soaring migrants is strongly affected also by wind conditions. Local radar and visual studies have shown that soaring migrants travel significantly faster when flying with tailwinds, while they travel slower when winds have an increasingly strong crosswind component (Kerlinger 1989, Spaar and Bruderer 1996, 1997a). Tracking studies have shown similar effects of wind persist along the entire migratory journey of soaring migrants (Shamoun-Baranes et al. 2003a, Mandel et al. 2008, Chevallier et al. 2010, Mellone et al. 2012).

Some raptors have more slender wings, such as harriers and falcons, and they are potentially less affected by weather conditions in comparison to obligate soaring migrants as they more frequently alternate soaring with flapping flight (facultative soaring migrants; Spaar and Bruderer 1997b). Consequently, they are able to continue migration during the night (Stark and Liechti 1993), and to some extent under adverse weather conditions (Spaar et al. 1998, Thorup et al. 2006). Furthermore, birds travelling by flapping are supported by tailwinds to the same extent as soaring birds, but are less affected by crosswinds as they lack the passive soaring flight phase during which birds may get fully drifted by crosswinds (Kerlinger 1989).

Even though aforementioned studies have revealed strong influences of wind and weather on the ground speeds of soaring migrants, these influences are rarely quantified simultaneously and, especially for entire migrations (Mandel et al. 2008). Satellite and GPS tracking studies on individual soaring migrants have revealed surprisingly similar patterns in hourly and daily speeds and daily travel distances achieved by different species of obligate as well as facultative soaring migrants (Trierweiler et al. 2007, Mandel et al. 2008, Chevallier et al. 2010, Mellone et al. 2012). For example, Palearctic soaring migrants typically achieve relatively high hourly speeds and longer daily travel distances over the Sahara (Kjellén et al. 2001, Klaassen et al. 2008, Chevallier et al. 2010, López-López et al. 2010) and it is often suggested that this is because birds may adjust their flight behavior over the hostile environment of this ecological barrier. Furthermore, several soaring migrants travel faster during spring migration compared to autumn (Mellone et al. 2012), possibly resulting from a seasonal urge to arrive early at their breeding sites (Kokko 1999, Nilsson et al. 2013). However, too little is known about the extent to which regional and seasonal performance relates to variation in the weather conditions encountered during travel (Tøttrup

et al. 2008). Recently, non-soaring, nocturnal migrants were shown to migrate faster over Europe in spring, compared to autumn, because tailwinds are more common in spring (Kemp et al. 2010). Furthermore, soaring birds like white storks *Ciconia ciconia* have been suggested to achieve higher speeds over the Sahara desert because relatively strong thermal convective conditions enable faster flights in this region (Shamoun-Baranes et al. 2003a). Also, more than half of the variation in travel performance of soaring Turkey vultures *Cathartes aura* can be explained from atmospheric conditions they encounter en route (Mandel et al. 2008). Overall, we expect the effects of weather conditions along entire migratory journeys may explain some of the seasonal or regional patterns in travel performance of (soaring) migrants.

We studied travel performance of two long-distance soaring migrants travelling along the East Atlantic flyway between Europe and Africa (Boere and Stroud 2006), using UvA-BiTS GPS-loggers (Bouten et al. 2012). Both species migrate at roughly the same time of the year, and thus encounter similar large-scale weather conditions during their travel, but use distinct migration strategies: the true soaring European honey buzzard *Pernis apivorus* (Bildstein 2006, Ferguson-Lees and Christie 2006) and the facultative soaring Montagu's harrier *Circus pygargus* (Spaar and Bruderer 1997b). We first describe general patterns in measured hourly speeds, mean daily speeds and daily travel distances, as well as in the weather conditions encountered for each species between different seasons and regions. Subsequently, we predict hourly speeds, daily speeds and daily distances from key weather conditions for soaring flight: boundary layer height (as a proxy for thermal convective conditions), precipitation, and wind conditions relative to the realized travel direction. We expected that boundary layer height should have a stronger positive effect on the hourly and daily performance of honey buzzards compared to Montagu's harrier, due to the aforementioned differences in their migration strategies. Finally, we add regional and seasonal factors to our weather models to explore whether any spatiotemporal behavioral patterns are not accounted for by weather conditions encountered en route.

Methods

Study species and GPS-tracking

Honey buzzards and Montagu's harriers are long-distance migratory birds breeding in temperate regions and wintering in sub-Saharan Africa (Ferguson-Lees and Christie 2006). Previous tracking studies using satellite transmitters revealed that autumn routes of adult honey buzzards breeding in Sweden converged in southern Spain to minimize the crossing of the Mediterranean Sea en route to tropical rainforests in western Africa (Hake et al. 2003). Tracking a large number of individual Montagu's harriers throughout Europe revealed western birds are using routes via Spain and Italy to their western Sahelian wintering quarters (Trierweiler et al. 2014). Both species migrate almost exclusively during daylight hours (Bruderer et al. 1994, Spaar and Bruderer 1997b). Montagu's harriers, however, may extend their travel into the night (Spaar and

Bruderer 1997b), especially during sea crossings (Limiñana et al. 2007, Trierweiler 2010).

We used UvA-BiTS GPS-loggers (Bouten et al. 2013) to track adult breeding birds, and thus experienced migrants. The honey buzzard was studied in two conifer-dominated (80% coniferous wood of which 74% *Pinus sylvestris*) areas in the center of the Netherlands (52.37°N, 5.82°E, van Manen et al. 2011). We trapped 13 individuals (Supplementary material Appendix 1, Table A1) at their nests with a mist net using a live or stuffed eagle owl *Bubo bubo* as a lure. Montagu's harriers were studied in their core breeding area in the Netherlands situated in the vast and open arable landscape of eastern Groningen (53.14°N, 07.03°E; Trierweiler 2010). We trapped four breeding birds near their nest with a pole trap or a mist net using a stuffed raptor decoy. GPS-loggers were fitted using Teflon or Tygontube harnesses (Kenward 1987, Snyder et al. 1989). Maximum mass of the harness and device amounted to maximum 5% of the bird's body mass. Birds were handled for less than 20–60 min after capture and so far we never observed nest desertion or failure related to our manipulations. GPS-locations were sampled at a resolution of 10 s to 1 h over the whole annual cycle. Data were downloaded in the breeding area through a combined fixed- and mobile relay-antennae system (Bouten et al. 2013).

Defining migration

For the full dataset spanning the entire annual cycle (> 500 000 GPS-locations) we first calculated ground speeds from every location to the next and to the previous point and then averaged these two speeds to calculate ground speed for each location. Based on the frequency distribution of ground speeds we identified and removed erroneous GPS-locations (ground speeds > 30 m s⁻¹).

In order to distinguish migration from other parts of the annual cycle we calculated daily travel distances as loxodrome distances between consecutive night roosts (first and last location obtained between 00:00 and 23:59 for each day). Based on histograms of daily distance we defined travel days as those days when more than 25 km was covered between roosts (cf. Klaassen et al. 2011). We only included travel days in our analyses, i.e. stopover days (days with daily distance < 25 km) were omitted.

Part of our study population of honey buzzards is known to exploit multiple wintering sites making itinerary movements (cf. Moreau 1972) between them (UvA-BiTS, unpubl.). Montagu's harriers also show within-year itinerancy (Trierweiler et al. 2013). In order to distinguish between travel days and itinerary movements we defined the onset and end of migration as the first and last set of travel days with a three-day running average daily travel distance of at least 65 km. Finally, we also left out pre- and post-migratory movements as these seem to differ from genuine migratory movements (Strandberg et al. 2008, Limiñana et al. 2012). We defined these as movements preceding or following a stop-over lasting at least three consecutive days within the breeding range (north of latitude 52°N) or near the wintering stages (south of latitude 25°N).

Our dataset contained 27 spring journeys and 22 autumn journeys for 13 honey buzzards and four spring and five

autumn journeys for four Montagu's harriers. Some travel days were not covered completely due to small gaps in the GPS data which in a few cases lead to an incorrect classification as stop-over day. In a few cases this misclassification was propagated when defining the core migration period based on the three-day running average of daily travel distance, in particular for honey buzzard #56 and Montagu's harrier #187 (Supplementary material Appendix 1, Table A1). We have chosen to leave the migratory travel days with some missing hourly values out of the analysis rather than to make assumptions to estimate these missing values. Less than 5% of the total data set was omitted because part of the hourly values within a day was missing. The number of migratory trips obtained per individual, species and season with the average number of travel days and travel distances that were retained are summarized in Supplementary material Appendix 1, Table A1.

Hourly speeds and daily distances

Safi et al. (2013) recommend using instantaneous speed measurements for studying animal movement ecology. However, it is not ideal to use instantaneous speeds for quantifying performance of soaring migrants as soaring flight consists of stages of circle-soaring in thermals alternated with glides between thermals (Kerlinger 1989) and instantaneous speeds during soaring and gliding do not accurately reflect cross-country performance (Kerlinger 1989). Instead, we defined hourly travel segments (described in more detail below) which are a good measure of short term ground speed because these segments include at least 5–10 complete soaring-gliding bouts (Kerlinger 1989, Leshem and YomTov 1996b, Spaar 1997). Furthermore, we expect that daily travel distance is a biologically meaningful scale of movement because soaring migrants are restricted to the daylight period for travel.

For every travel day, we used a minimum ground speed of 1.5 m s⁻¹ between two consecutive measurements to determine the start and end of the daily travel period. Subsequently, we resampled the whole dataset, creating 1 h segments, by retaining consecutive locations with a time difference as close to one hour as possible (minimum and maximum segment duration was 50 and 70 min, respectively). Hourly speeds (m s⁻¹) were recalculated after resampling, and hourly speeds lower than 1.5 m s⁻¹ were classified as resting events, which were omitted from the hourly travel performance analyses. 7583 and 1376 hourly travel segments were obtained for honey buzzards and Montagu's harriers, respectively.

After resampling, we also recalculated daily distances, as the loxodrome distance between the first and last hourly location of the daily travel period. The final dataset contained 1223 and 205 daily distances for honey buzzards and Montagu's harriers, respectively.

Daily mean speeds and the role of travel time

Daily travel distance is the sum of hourly speeds over the daily travel time, thus daily travel time has a profound effect on daily distance (Klaassen et al. 2008). The length of the daylight period, and thus the length of the period with favorable

soaring conditions, varies considerably across the migration period, particularly in spring (Mellone et al. 2011, 2012). Furthermore, migrants may interrupt flights (e.g. for foraging or to avoid rain or strong headwinds; Thorup et al. 2006) or may extend their daily travel period through dusk and dawn (Stark and Liechti 1993, Spaar and Bruderer 1997b, Limiñana et al. 2007, Trierweiler 2010). As our aim is to quantify the effect of weather on performance while travelling, we predict daily distance based on those conditions encountered during travel hours only. In order to adjust for variation in daily travel times we also calculated daily mean travel speeds. Comparing daily mean speeds with daily distances allows for a better understanding of the role of travel time in shaping daily travel performance.

Regional and seasonal patterns in weather conditions and performance

In order to evaluate regional and seasonal patterns in migration performance and weather conditions encountered by the birds we used an ANOVA and a Tukey's HSD. A t-test was used to compare the two seasons. In both cases differences with a p-value of 0.05 or lower were considered significant.

We used the borders of global biomes (Olson et al. 2001) to distinguish six regions in terms of their geographical position and their characteristic vegetation: temperate forests (broad-leaf and coniferous forest in Europe), Mediterranean (including subtropical grasslands north of 25°N), sea, desert, tropical grasslands (including flooded savannas), and tropical rainforest (rainforest and mangroves).

If birds change their behavior above different regions we want to ignore those segments during which birds crossed from one region into another. We, therefore, subset our data to hourly speeds determined over segments where a bird was continuously travelling over the same region (i.e. start and end location fell within the same region), and for days during which at least 60% of the hourly segments was spent over the same region.

Modeling weather effects

The response variables in our study are hourly speed, daily mean speed and daily distance. We adopted a backward model selection procedure including four predictor variables (boundary layer height, tailwind, absolute crosswind and precipitation) in our initial linear regression model for hourly speeds and three predictor variables (mean daily boundary layer height, tailwind and absolute crosswind) in our initial regression model for daily distance and daily mean speed. During variable selection, predictor variables with a p-value lower than 0.05 were removed starting with the least significant variable until all remaining variables were significant. In order to compare the relative importance of between predictor variables (i.e. relative effect sizes) we additionally fitted the final models based on normalized response and predictor variables, i.e. for each model we standardized all variables to units of standard deviation after which linear regression coefficients yielded effect sizes showing the change of the response variable in units of SD, for every unit of SD change in one of the predictor variables.

We obtained boundary layer height (m), u- and v-wind components (i.e. latitudinal and longitudinal wind velocities, m s^{-1}) and the accumulated rainfall (mm) from the ECMWF (European Center for Medium-Range Weather Forecasts) regional atmospheric model at a resolution of 0.25° and 3 h (Anderson 2013). Data were linearly interpolated in space and time for each hourly location. Boundary layer height is a good approximation of convection at hourly to daily scales as a higher boundary layer is associated with stronger thermals (allowing faster and higher climbs during soaring), as well as with more dense thermal fields (Stull 1988), both of which are likely to affect the performance of soaring migrants (Spaar et al. 2000, Shannon et al. 2002, Shamoun-Baranes et al. 2003a, b).

Wind strength and direction may vary strongly with altitude above the ground (Stull 1988) and the ECMWF regional atmospheric model grid provides conditions at different barometric pressure levels relative to sea level (i.e.: at 10 m above the sea, and at pressure levels 925, 850 and 700 mB). Therefore, we first calculated hourly flight direction to determine hourly tailwind and crosswind components (cf. Chevallier et al. 2010) at each pressure level, and then linearly interpolated tailwind and crosswind components from the two pressure levels nearest to the bird's effective flight altitude. The two closest pressure levels were determined based on the vertical distance between the geopotential heights of the pressure levels (available in ECMWF) and the bird's altitude above the sea. ECMWF precipitation data represent accumulated rainfall over three-hour periods, hence we used an estimate for hourly rainfall by dividing the ECMWF-scores by three.

We determined mean daily values for each predictor variable across all hourly travel segments between 00:00 and 23:59, and so excluding all resting hours. In order to obtain daily tailwind and crosswind components we calculated the tailwind and absolute crosswind component at each hourly location relative to the daily mean axis of movement before we averaged each component across each day. We then predicted daily distance in function of daily mean boundary layer height, mean tailwind and mean absolute crosswind. We did not analyze the effect of precipitation at the daily scale because the strongest effect of precipitation on daily distance likely comes from birds interrupting travel altogether under rainy conditions (Kerlinger 1989, Thorup et al. 2006).

Regional and seasonal differences in response to weather

In order to identify potential differences in response to weather between different regions and seasons we describe and compare regional and seasonal patterns in predicted and observed performance. Furthermore, we test whether any significant additional variation in performance can be explained by regional or seasonal effects that are not accounted for by weather conditions. To do so, we compare three extended versions of the final weather models for each response variable for each species, by including region, season or both factors together as additional predictor variables. We then use Aikake's information criterion (AIC) to compare model fit, and Pearson's R to compare the amount of variation explained between models.

All statistical modeling was conducted in the program R 2.15.0 (R Core Development Team), using the ggplot2 package (Wickham 2009) for graphical representation of results.

Results

Honey buzzards on average spent 25 d to migrate between their breeding grounds in the center of the Netherlands and their individual wintering grounds across tropical West to Central Africa (Supplementary material Appendix 1, Table A1). They usually crossed the Mediterranean Sea in one to two hours at its narrowest point at the Strait of Gibraltar (Fig. 1A, I). Two birds flew parallel to the eastern Spanish coast for 3 and 6.5 h, respectively, in spring 2010. However, these birds also continued to travel over land on those days such that honey buzzards never spent an entire day only over the sea (Supplementary material Appendix 1, Table A1). These events were not plotted in Fig. 1a since we only plotted hourly locations when at least 60% of daily travel time was spent over the same biome. When crossing the desert, some honey buzzards made notable detours deviating east (both autumn and spring) or west (spring) from their initial heading (Fig. 1A, I, Supplementary material Appendix 1, Table A1). One occasion involving two birds suggests the birds detoured in avoidance of a dust storm (Treep 2012). Honey buzzards travelled short distances over the rain forests so relatively few travel segments were obtained there (Fig. 1A, I, Table 1). Montagu's harriers travelled about 28 d to reach their wintering grounds in the Sahel in Senegal and Niger. Two used a westerly route via Spain and two others flew over the central Mediterranean (Fig. 1B, I, note one spring journey was removed almost entirely during data processing due to frequent gaps in data). They travelled only short distances over the Sahel, so we have a relatively small sample over tropical grasslands (Fig. 1B, I). On two occasions Montagu's harriers made long autumn sea-crossings lasting up to 19 h. In spring the harriers used islands as stepping stones while migrating between Africa and the Italian peninsula (Fig. 1B, I).

Seasonal and regional patterns in encountered weather conditions

Weather conditions differed between regions and in some regions also between seasons (Supplementary material Appendix 1, Fig. A2a, b, and Table A3). However, Montagu's harriers only encountered seasonally different hourly tailwinds, while all hourly and daily conditions encountered by honey buzzards differed between seasons. Largest differences in mean conditions were usually tenfold the size of the variance in mean conditions per region and season. For example, honey buzzards encountered significantly more crosswinds over the desert and more frequent tailwinds over Europe in spring than in autumn (Supplementary material Appendix 1, Fig. A2a, b, Table A3). Crossing the Sahara, honey buzzards experienced hourly and daily mean boundary layer heights reaching about 700 m lower in spring compared to autumn. Moreover, the boundary layer heights they encountered were much lower over the tropical

grasslands and forests in autumn compared to spring, likely because of frequent autumn rains in those areas (Supplementary material Appendix 1, Fig. A2a, Table A3).

Seasonal and regional patterns in performance and travel time

Honey buzzards showed a significant difference in migratory performance between regions and seasons (Fig. 1A, II–IV, Table 1, 2) at both the hourly and the daily scale. Honey buzzards travelled consistently faster and further during spring than during autumn migration. Within seasons, the highest regional hourly and daily speeds and daily distances were achieved above the Sahara (Fig. 1A, II–IV, Table 1). In autumn, honey buzzards achieved higher hourly speeds above sea compared to the average over terrestrial regions (Fig. 1A, II). In both seasons, shortest daily distances were reached above rainforest (Fig. 1A, III) because they achieved moderately lower daily mean travel speeds (Fig. 1A, IV) and because they travelled for about 1–3 h less per day, compared to elsewhere in Africa and the Mediterranean.

Overall, performance of Montagu's harriers did not differ significantly between seasons (Table 2), but hourly speeds and daily distances were lowest on arrival in the Sahel, and highest among the terrestrial habitats on departure from the Sahel (Fig. 1B, II, III). Daily mean speeds were more or less consistent across terrestrial regions (Fig. 1B, IV, Table 1). In autumn, Montagu's harriers achieved the lowest daily distance and travel times above tropical grasslands of the Sahel. In spring, daily mean speeds and travel times were lowest in the temperate region. Furthermore, they achieved far greater daily distance and travel time over open sea than over any other area (Fig. 1B, III, V, Table 1).

Weather effects on performance

The final models are given for honey buzzards in Table 3a and for Montagu's harriers in Table 3b. The full models before backward model selection are shown in Supplementary material Appendix 1, Table A4, including the significance and normalized regression coefficients for each weather variable. Variation in weather conditions predicted 48% of the variability in hourly speeds, 41% of variation in daily distances and 32% of variation in daily mean speeds achieved by honey buzzards. For Montagu's harriers, our final weather models predicted 42% of the variation in hourly speeds, 33% of variation in daily distances and 32% of variation in daily mean speeds.

The effects of weather on hourly speed were similar for both species, with a dominant positive influence of tailwinds, an additional positive effect of boundary layer height, and a negative effect of absolute crosswinds (Table 3a, b). Honey buzzards travelled significantly slower at the hourly scale with increasing rainfall, although they travelled in weak to moderate rains (Supplementary material Appendix 1, Fig. A2a, Table 3a) which only had a small influence on hourly travel speeds compared to other weather variables (Table 3a). Precipitation had no effect on the hourly performance of Montagu's harriers (Tables 3a, b, Supplementary material Appendix 1, Table A4).

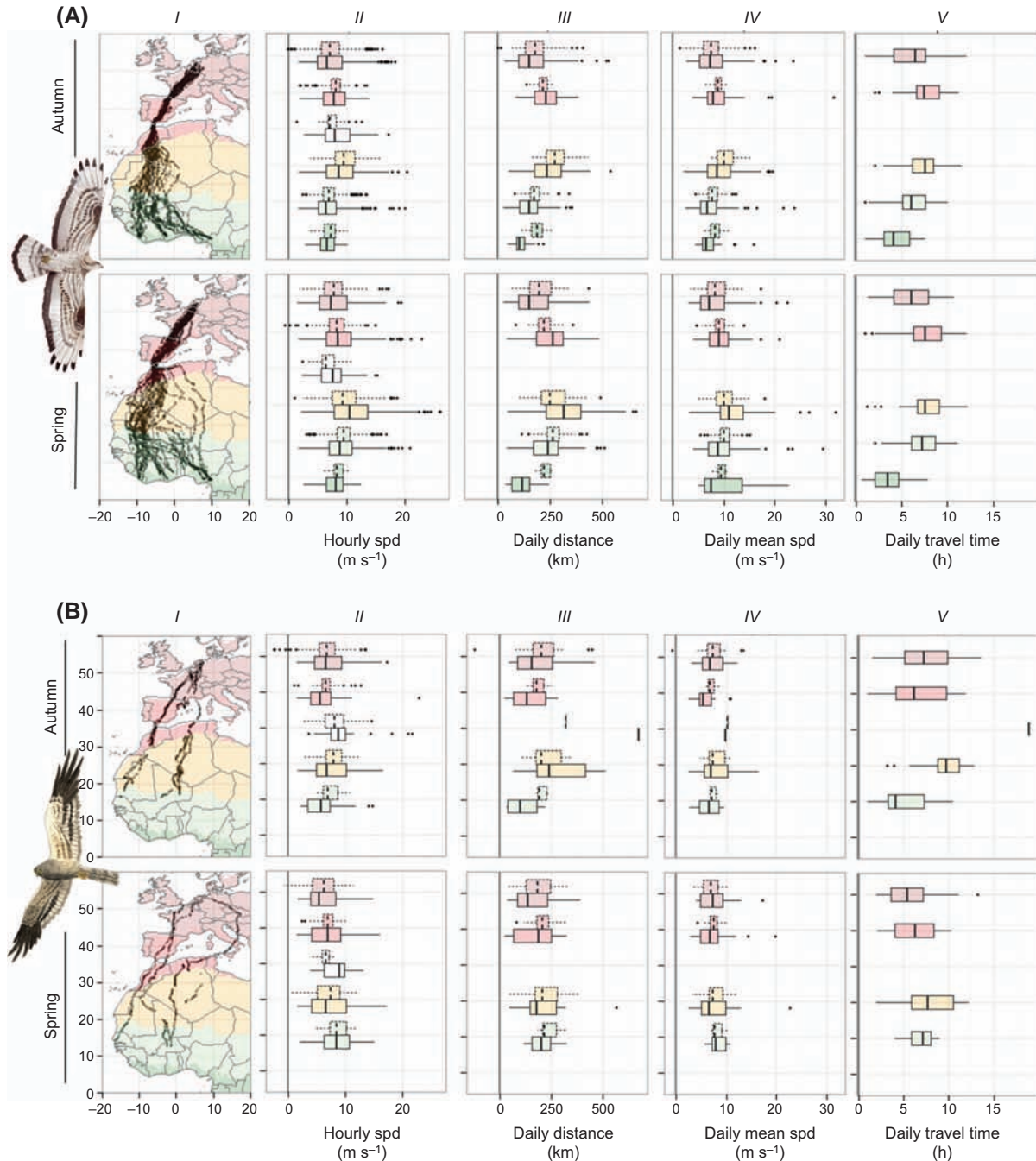


Figure 1. Migration routes (I), hourly travel speeds (II), daily travel distance (III), daily mean travel speed (IV) and daily travel times (V) of honey buzzards (A) and Montagu's harriers (B) for autumn (top panels) and spring (bottom panels) migrations respectively. Migration routes are plotted as the hourly locations (semi-transparent points) from all travel days. Box-plots show mean (bold line) and spread of values (box bounds = inter-quartile range of values from the 25th to the 75th percentile, whiskers = 1.5*inter-quartile range) with outliers (dots). Full box-plots show distributions of observed values and dashed box-plots show predicted values for each variable. Colours of box-plots and in background of migration routes indicate different regions (Table 1).

The daily distance and daily speed of honey buzzards was determined by daily mean tailwind and added effects of daily mean boundary layer height and crosswinds, whereas the performance of Montagu's harriers was affected only by tailwind at the daily scale (Table 3a, b).

For honey buzzards the normalized effect of tailwinds on hourly speed, daily distance and daily mean speed was almost two times as large as the normalized effect of boundary layer

height, and almost 5 times larger than the normalized effect of absolute crosswinds (Supplementary material Appendix 1, Table A4), showing that tailwinds have a much stronger influence on migration performance than other weather variables. For Montagu's harriers the normalized effect of tailwinds on hourly speeds was three times the normalized effect of boundary layer height (Supplementary material Appendix 1, Table A4).

Table 1. Regional patterns in hourly speed, daily distance and daily mean speed as observed from GPS-tracking and as predicted from weather conditions encountered en route of migration (see Table 2 for models), during autumn and spring migration of honey buzzards and Montagu's harriers respectively. Class identifiers (a–f) were determined by a Tukey-HSD test for each variable in both species to identify those biomes over which speeds or distances were significantly similar.

Species	season	Biome	Hourly speed				Daily distance				Daily speed			
			n	obs	obs class	pred	n	obs	obs class	pred	n	obs	obs class	pred
Honey buzzard	autumn	Temp forest	764	7.19	d	7.08	122	171.57	cd	177.48	122	7.91	cd	7.63
		Mediterr	828	7.65	d	7.96	76	227.53	b	214.88	76	8.81	bcd	8.78
		Sea	29	8.44	bcd	7.38	–	–	–	–	–	–	–	–
		Desert	886	8.79	bc	9.61	109	237.85	b	277.52	109	9.27	bc	10.39
		Trop grass	1011	6.7	d	6.92	163	153.1	cd	176.38	163	7.54	d	7.77
	spring	Trop forest	169	6.55	d	7.03	35	102.7	d	185.43	35	7.07	d	8.27
		Temp forest	838	7.62	d	7.68	140	172.1	cd	199.97	140	8.09	bcd	8.46
		Mediterr	911	8.56	bc	8.19	86	244.36	b	219.72	86	9.33	bc	9.11
		Sea	55	7.53	d	6.59	–	–	–	–	–	–	–	–
		Desert	905	10.77	a	9.51	103	318.98	a	261.24	103	11.78	a	10.32
		Trop grass	1004	8.96	b	9.34	129	233.62	b	260.54	129	9.43	b	10.09
		Trop forest	183	7.83	cd	8.35	26	135.39	cd	222.47	26	8.9	bcd	9.42
	autumn	Temp forest	219	7.09	bc	6.63	28	177.35	c	204.76	28	7.18	a	7.4
		Mediterr	235	5.8	d	6.56	25	152.55	c	189.2	25	5.94	a	7.01
		Sea	46	9.39	a	8.12	2	556.49	a	320.16	2	10.01	a	10.29
		Desert	273	7.51	abc	7.96	26	277.58	b	226.34	26	8.12	a	7.94
		Trop grass	42	5.99	cd	7.47	6	116.77	c	203.79	6	6.37	a	7.37
	spring	Temp forest	138	6.29	cd	5.96	19	165.18	c	185.59	19	7.84	a	6.92
		Mediterr	147	7.09	bc	6.89	20	161.02	c	207.86	20	7.71	a	7.47
		Sea	30	8.27	abc	6.42	–	–	–	–	–	–	–	–
		Desert	172	7.44	abc	7.09	21	209.5	bc	216.03	21	8.13	a	7.68
		Trop grass	70	8.36	ab	8.45	7	206	bc	240.37	7	8.34	a	8.29

Regional and seasonal differences in the influence of weather

The predicted seasonal and regional patterns in hourly speed, daily distance and daily speed overall closely matched the patterns we observed for both species (Fig. 1A, II–IV; Table 1). Region and season accounted for less than 1% of the variation in hourly and daily speeds of either species when weather effects were accounted for (Table 3a, b). These small regional effects do not improve the overall predictive ability of our hourly and daily speed models because the influence of weather is much greater (Table 3a, b). Regional effects did explain ca 7 and 13% additional variation in daily

distances which was not accounted for by weather conditions encountered by honey buzzards and Montagu's harriers respectively. Seasonal differences, however, only accounted for about 2% of all variation in daily travel distance.

Honey buzzards reached consistently higher speeds than predicted over the sea (Fig. 1A, II, Table 1). Furthermore, daily distances travelled by honey buzzards are consistently lower than predicted above the tropical forests, whereas this is not the case for daily speeds (Fig. 1A, III–IV), indicating that they seem to make frequent short stops there. For Montagu's harriers, daily distances achieved over the sea were much higher than predicted due to extremely long travel times (Fig. 1B, II–III; Table 1). Furthermore, daily distances

Table 2. Seasonal averages, and differences therein (student's t-test), of hourly speed, daily distance and daily mean speed as observed from GPS-tracking and of hourly and mean daily weather conditions encountered by honey buzzards and Montagu's harriers respectively. p-values of significant seasonal differences ($p < 0.05$) are highlighted in bold.

	Hourly scale				Daily scale			
	autumn	spring	seas. diff	p	autumn	spring	seas. diff	p
Honey buzzard								
Speed (m s^{-1})	7.51	8.95	1.29 <=> 1.59	<2.2E-16	8.28	9.62	0.89 <=> 1.76	3.11E-13
Distance (km)	–	–	–	–	193.33	238.41	33.09 <=> 57.08	3.11E-13
Boundary layer height (m)	1656.21	1719.55	19.37 <=> 107.31	4.76E-04	1670.77	1808.27	49.34 <=> 225.67	2.26E-03
Tailwind (m s^{-1})	–0.21	1.27	1.32 <=> 1.63	<2.2E-16	–0.51	0.93	1.06 <=> 1.82	2.45E-13
Absolute crosswind (m s^{-1})	2.69	3.41	0.61 <=> 0.85	<2.2E-16	2.63	3.54	0.64 <=> 1.18	4.14E-11
Precipitation (mm)	0.22	0.11	–0.13 <=> –0.08	<2.2E-16	–	–	–	–
Montagu's harrier								
Speed (m s^{-1})	6.96	7.22	–0.13 <=> 0.65	0.20	7.12	7.94	–0.30 <=> 1.96	0.15
Distance (km)	–	–	–	–	204.72	182.10	–61.36 <=> 16.11	0.25
Boundary layer height (m)	1638.99	1623.59	–143.59 <=> 112.81	0.81	1686.38	1700.16	–236.51 <=> 264.08	0.91
Tailwind (m s^{-1})	1.29	0.68	–1.09 <=> –0.14	0.01	0.58	0.31	–1.51 <=> 0.97	0.67
Absolute crosswind (m s^{-1})	2.97	2.96	–0.27 <=> 0.26	0.98	3.18	3.44	–0.45 <=> 0.96	0.48
Precipitation (mm)	0.11	0.12	–0.04 <=> 0.06	0.69	–	–	–	–

Table 3a. Final linear regression models for hourly speed, daily mean speed and daily distance of honey buzzards in function of significant weather variables and three extended models testing for additional regional or seasonal effects not accounted for by weather conditions. Regional and seasonal factors to not improve model fit (AIC) nor the amount of variation explained (R^2), except for daily distance models where regional effects account for up to 6% more of total variation than can be explained by weather conditions.

Model	Predictor	Hourly speed (m s ⁻¹)				Daily speed (m s ⁻¹)				Daily distance (km)			
		Eff. size	p	AIC	R ²	Eff. size	p	AIC	R ²	Eff. size	p	AIC	R ²
~ weather	WEATHER: Int.	6.492	<2E-16	32780	0.48	7.740	<2E-16	4662	0.32	146.661	<2E-16		
	Blh	1.18E-03	<2E-16			9.00E-04	6.41E-11			0.046	<2E-16		
	Tailwind	0.572	<2E-16			0.600	<2E-16			16.318	<2E-16	10439	0.41
	Crosswind	-0.159	<2E-16			-0.180	1.91E-04			-5.433	9.44E-06		
	Rain	-0.225	4.10E-05			–	–			–	–		
~ weather + region	WEATHER: Int.	6.978	<2E-16	32699	0.49	8.666	<2E-16	4659	0.33	205.300	<2E-16		
	Blh	1.35E-03	<2E-16			7.84E-04	1.59E-06			0.003	<2E-16		
	Tailwind	0.562	<2E-16			0.603	<2E-16			15.900	<2E-16	10352	0.47
	Crosswind	-0.181	<2E-16			-0.206	3.71E-05			-6.710	3.23E-08		
	Rain	-0.138	0.013			–	–			–	–		
	REGION: Mediter	-0.323	2.38E-04			-0.353	0.352			-3.078	0.737		
	Sea	0.685	0.014			–	–			–	–		
	Temp for	-0.353	1.19E-04			-0.582	0.106			-43.410	7.31E-07		
	Trop for	-0.958	4.49E-08			-1.111	0.080			-121.200	7.80E-15		
	Trop grass	-0.689	6.21E-16			-1.016	2.51E-03			-48.590	3.25E-09		
	WEATHER: Int.	6.837	<2E-16	32668	0.49	8.090	<2E-16	4659	0.33	162.111	<2E-16		
	Blh	1.17E-03	<2E-16			9.22E-04	1.53E-10			0.045	<2E-16		
~ weather + season	Tailwind	0.555	<2E-16			0.596	<2E-16			15.662	<2E-16	10425	0.42
	Crosswind	-0.172	<2E-16			-0.197	5.23E-05			-6.186	5.15E-07		
	Rain	-0.170	1.84E-03			–	–			–	–		
	SEASON: Autumn	-0.637	<2E-16			-0.532	2.01E-02			-23.457	5.21E-05		
	WEATHER: Int.	7.385	<2E-16	32579	0.49	9.099	<2E-16	4656	0.34	223.500	<2E-16		
~ weather + season + region	Blh	1.12E-03	<2E-16			7.49E-04	4.64E-06			0.031	2.84E-15		
	Tailwind	0.546	<2E-16			0.585	<2E-16			15.170	<2E-16		
	Crosswind	-0.194	<2E-16			-0.222	1.02E-05			-7.384	1.28E-09		
	Rain	-0.082	0.139			–	–			–	–		
	SEASON: Autumn	-0.655	<2E-16			-0.549	0.017			-23.120	3.24E-05	10337	0.48
	REGION: Mediter	-0.371	2.15E-05			-0.430	0.256			-6.343	0.487		
	Sea	0.621	0.025			–	–			–	–		
	Temp for	-0.416	5.00E-06			-0.679	0.060			-47.500	5.73E-08		
	Trop for	-0.962	3.06E-08			-1.086	0.086			-120.200	7.54E-15		
	Trop grass	-0.736	<2E-16			-1.057	1.66E-03			-50.280	6.89E-10		

achieved by Montagu's harriers, which frequently interrupted travel over the tropical grasslands, were lower than predicted by tailwinds (Fig. 1B, III; Table 1). In contrast, predicted daily mean travel speeds were accurate over the grasslands of the Sahel as well as over the sea (Fig. 1B, IV; Table 1).

Diurnal patterns in hourly speeds

We observed a striking diurnal pattern in the accuracy of prediction of hourly speeds with a tendency for both species to migrate slower than predicted at sunrise and sunset, most notably so for honey buzzards which tend to wait for thermal convection to develop after sunrise (Fig. 2).

Discussion

Species-specific weather effects

Our results show that weather explains between 40 and 50% of the variation in hourly speeds and between 30 and 40% of variability in daily distances and daily mean speeds achieved

by soaring migrants. We show that wind conditions as well as boundary layer height, which reflects the depth of the atmospheric boundary layer in which thermal convection develops and how high birds can climb while soaring (Spaar et al. 2000, Shamoun-Baranes et al. 2003b), are important determinants of hourly travel performance for honey buzzards and Montagu's harriers along their entire migratory journey. Previously the influence of both wind and convective conditions on soaring flight was observed for our study species only from single-site studies (Bruderer et al. 1994, Spaar 1997, Spaar and Bruderer 1997a, b, Shamoun-Baranes et al. 2003b). Some authors have compared the travel speed of broad-winged hawks in the Americas and honey buzzards in Europe between a northern and southern location along their respective migration flyways and also found that travel performance was higher at southern latitudes where thermal soaring conditions were better (Bruderer et al. 1994, Careau et al. 2006). Moreover, black storks *Ciconia nigra* migrating between Europe and Africa, and Swainson's hawks *Buteo swainsoni* migrating over the Americas, like our study species, also achieved higher hourly ground speeds at southern latitudes, most likely due to better thermal convective

Table 3b. Final linear regression models for hourly speed, daily mean speed and daily distance of Montagu's harriers in function of significant weather variables and three extended models testing for additional regional or seasonal effects not accounted for by weather conditions. Regional and seasonal factors to not improve model fit (AIC) nor the amount of variation explained (R^2), except for daily distance models where regional effects account for up to 13% more of total variation than can be explained by weather conditions.

Model	Predictor	Hourly speed (m s^{-1})				Daily speed (m s^{-1})				Daily distance (km)			
		Eff. size	p	AIC	R^2	Eff. size	p	AIC	R^2	Eff. size	p	AIC	R^2
~ weather	WEATHER:	Int.	6.045	<2E-16	6162	0.42	7.214	<2E-16	713	0.32	188.281	<2E-16	
		Blh	5.61E-04	<2E-16			—	—			—	—	
		Tailwind	0.493	<2E-16			0.473	2.10E-13			17.041	2.03E-13	
		Crosswind	-0.138	1.10E-05			—	—			—	—	
~ weather + region	WEATHER:	Int.	5.570	<2E-16	6122	0.44	7.590	<2E-16	718	0.33	232.729	<2E-16	
		Blh	7.29E-04	<2E-16			—	—			—	—	
		Tailwind	0.494	<2E-16			0.468	1.18E-12			15.278	1.09E-12	
		Crosswind	-0.153	1.52E-06			—	—			—	—	
	REGION:	Mediterr	-0.066	0.751			-0.970	0.128			-77.571	2.55E-04	1714 0.45
		Sea	1.977	1.40E-07			-0.698	0.813			344.001	4.75E-04	
		Temp for	0.745	3.35E-04			-0.112	0.857			-53.049	0.010	
		Trop grass	-0.469	0.096			-0.666	0.481			-85.783	0.006	
~ weather + season	WEATHER:	Int.	6.361	<2E-16	6150	0.42	7.720	<2E-16	711	0.34	177.469	<2E-16	
		Blh	5.68E-04	<2E-16			—	—			—	—	
		Tailwind	0.498	<2E-16			0.474	1.29E-13			17.014	2.18E-13	
		Crosswind	-0.138	9.90E-06			—	—			—	—	
	SEASON:	Autumn	-0.579	1.25E-04			-0.906	0.062			19.347	0.270	
~ weather + region + season	WEATHER:	Int.	5.943	<2E-16	6105	0.45	8.160	<2E-16	716	0.35	226.604	<2E-16	
		Blh	7.42E-04	<2E-16			—	—			—	—	
		Tailwind	0.500	<2E-16			0.468	7.36E-13			15.273	1.25E-12	
		Crosswind	-0.155	9.30E-07			—	—			—	—	
	SEASON:	Autumn	-0.650	1.46E-05			-0.966	0.049			10.376	0.519	1716 0.45
	REGION:	Autumn	-0.091	0.658			-1.021	0.106			-77.014	2.94E-04	
		Mediterr	—	—			-0.305	0.917			339.786	5.85E-04	
		Sea	1.931	2.24E-07			-0.124	0.840			-52.921	0.010	
		Temp for	0.756	2.48E-04			-0.834	0.375			-83.974	0.008	
		Trop grass	-0.644	0.023			—	—			—	—	

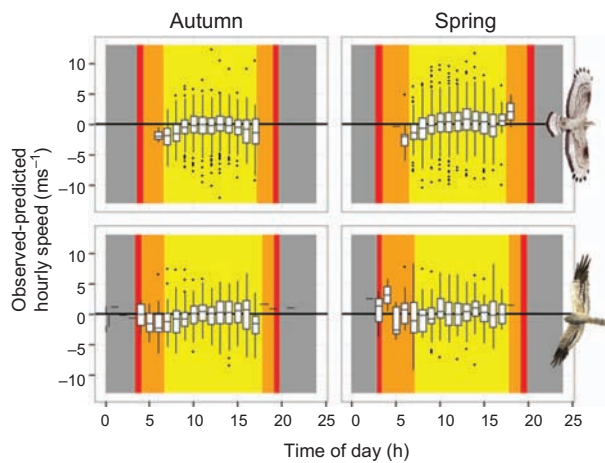


Figure 2. The diurnal pattern of the difference between predicted and observed hourly speeds for honey buzzards (top panels) and Montagu's harriers (bottom panels) during autumn (left panels) and spring (right panels) respectively. For each season we calculated minimum and maximum dawn, sunrise, sunset and dusk times encountered by all birds. The daytime period is shown in yellow, between the latest sunrise and earliest dawn encountered throughout either season for each species. Orange indicates range between earliest and latest sunrise and sunset times, while red zones indicate earliest and latest twilight periods in each season. Night time is shown in grey, between the latest dusk and the earliest dawn experienced during migration.

conditions (Fuller et al. 1998, Chevallier et al. 2010). Turkey vultures *Cathartes aura*, breeding in North America, were shown to be affected strongly by 'turbulent kinetic energy' (a proxy for vertical atmospheric energy, including thermal convection) and wind strength for migration (Mandel et al. 2008) along their entire journeys. Unlike most of these studies, however, we explicitly quantified the relative effects of different weather variables on performance, showing that tailwind is the highly dominant factor affecting daily travel distance of both an obligate and a facultative soaring migrant along the entire flyway (cf. Mellone et al. 2012). Honey buzzards were more sensitive to variation in boundary layer height than Montagu's harriers, which we expected because harriers may modulate their flight time substantially for reasons other than optimizing travel performance as a function of convective conditions (Spaar and Bruderer 1997b, Limiñana et al. 2007). Our results also show that the hourly speeds of facultative soaring Montagu's harriers are less affected by variation in crosswind than honey buzzards. We expected this because harriers could overcome crosswinds rather efficiently by switching to flapping flight (Limiñana et al. 2013) compared to honey buzzards which we expect to refrain from such energetically costly flapping, even if they then must accept some drift from their intended travel direction.

Moreover, we provide evidence that a true soaring species travels faster and further with stronger average daily thermal convection (Spaar et al. 2000, Shamoun-Baranes et al.

2003a, Mandel et al. 2008, Chevallier et al. 2010). Harriers, however, extended their daily travel time in the absence of suitable soaring conditions, during early morning and after dusk, thereby reducing their reliance on daily boundary layer conditions (Limiñana et al. 2007, Klaassen et al. 2008). The absence of a crosswind effect on daily speeds and travel distances of harriers is consistent with our expectation that facultative soaring migrants would more readily use flapping flight to compensate for drift and thus fly at higher ground speeds than possible during soaring flight.

Regional and seasonal patterns in migration performance and weather conditions

When accounting for weather conditions on the way, no more large differences were found in the performance of soaring migrants, neither among terrestrial regions nor between seasons. Thus we show that seasonal flight speeds of soaring migrants are not primarily due to a seasonal change in behavior as often suggested for higher migration speeds noted in spring compared to autumn (Kokko 1999, López-López et al. 2010, Nilsson et al. 2013), but are rather predominantly the effect of weather conditions encountered during flight (Tøttrup et al. 2008, Kemp et al. 2010). The small regional differences in migration speeds which we could not explain from weather conditions could arise from regional variation in flight orientation, foraging strategies, airspeeds or a combination of changes in flight behavior. A recent study showed that soaring migrants passing over Israel adjust their gliding airspeeds to thermal soaring conditions, but that they glide more slowly than expected in order to stay in the air longer during the gliding phase, thereby increasing the chance of reaching the next thermal without the need to resort to flapping (Horvitz et al. 2014). Such a risk-averse strategy may be more important in regions or seasons with relatively poor soaring conditions, and thus soaring migrants may adjust their airspeeds to soaring conditions differently between different regions or seasons. However, we expect the effect would be small in comparison to the strong influence of wind. Given this strong dependence on weather, soaring migrants may most efficiently influence their performance by choosing the best available atmospheric flows for travel. To do so, they could interrupt their travel under disadvantageous conditions (Thorup et al. 2006), or orient themselves in the best possible angle relative to the wind in order to maximize the progress they make toward their destinations (Klaassen et al. 2011).

While both species reduced their travel time and speeds when approaching seasonal destinations (e.g. when reaching the Sahel in autumn, and when reaching the temperate forest in spring), these patterns are accounted for by weather conditions, and so we suspect the birds were not flying slower because they were relaxing while approaching their destinations (Meyburg et al. 1995, Fuller et al. 1998). Only above sea we consistently underestimated the hourly and daily performance for both species. The general absence of thermals over large water bodies in the temperate zones prohibits stationary circle-soaring there and requires soaring migrants to cross water bodies using flapping flight (Kerlinger 1989, Bildstein 2006, Bildstein et al. 2009). We actually would expect that a transition to flapping flight lead

to higher ground speeds than predicted from our model, given the model was parameterized on predominantly continental soaring migration data. Behavioral information from accelerometers integrated in tracking devices can help to distinguish flapping from soaring flight events to generate a more complete understanding of how weather influences these migrants (Bouten et al. 2013, Liechti et al. 2013).

The role of travel time

Remaining differences in daily travel distance between regions (7–13% of total variation for honey buzzard and Montagu's harrier respectively) show that daily performance is affected by how soaring migrants modulate their travel time. Honey buzzards, for example, travelled much shorter distances than predicted above tropical forests (Fig. 1, Table 1), probably because they frequently interrupted their travels there due to precipitation (Thorup et al. 2006). Montagu's harriers reduced their daily travel time, hourly speeds and daily distances over the Sahel in autumn and over the Mediterranean region in spring, likely because they were foraging there to replenish their energy reserves (Trierweiler et al. 2007, Limiñana et al. 2012). Other fly-forage migrants such as ospreys *Pandion haliaetus* also vary their travel and feeding schedules depending on regional and seasonal energy requirements (Klaassen et al. 2008). In addition, the birds may have reduced their daily travel time because they arrived close to their seasonal destinations (Meyburg et al. 1995, Fuller et al. 1998).

Montagu's harriers travelled much further per day over the sea than predicted by weather conditions, because they did not interrupt travel during sea-crossings in the central Mediterranean, even when stepping stones were available as in spring (Fig. 1B, I, V), and continued to fly even when soaring conditions were not available. Interestingly, winds experienced by Montagu's harriers during sea-crossing were significantly weaker in spring than in autumn, with a lower proportion of strong crosswinds (Supplementary material Appendix 1, Fig. A2a, b). This suggests that, similar to marsh harriers (Klaassen et al. 2010), some Montagu's harrier may have evolved a seasonal loop migration, whereby they avoid a detour in spring by crossing the Mediterranean directly, as winds are more favorable for sea-crossings in that season. Montagu's harriers that do make sea-crossings in autumn tend to select specific wind conditions to do so (Meyer et al. 2000).

Overall, the take-off and stop-over decisions of soaring migrants, which determine their daily travel times, seem more influential for overall daily performance than modulations in flight speed (Nilsson et al. 2013). This finding stresses the need for further research on how precipitation and other weather factors may affect the daily time budgets of soaring migrants (Thorup et al. 2006, Klaassen et al. 2008).

The role of orientation and wind

There are only small regional patterns remaining in hourly speeds that are not accounted for by weather, nor by travel time. Honey buzzards, for example, achieved consistently higher hourly speeds than predicted in spring, and migrated consistently slower than predicted in autumn (Fig. 1A, II–IV, Table 1). The fast Sahara-crossing in spring is clearly

related to stronger winds over the desert during spring (Supplementary material Appendix 1, Table A3a, Fig. A2a) which enabled honey buzzards to reach higher ground speeds than they could under the stronger convective conditions over the Sahara in autumn (Supplementary material Appendix 1, Table A3a, Fig. A2a). However, the honey buzzards should also compensate relatively more for winds during (the last stage of) the desert crossing in spring while they navigate towards the Gibraltar Strait (Klaassen et al. 2011) whereas they seem to drift with prevailing winds over the Sahara in autumn. If honey buzzards are held back more by side winds when compensating, than otherwise, we should expect our model, which was parameterized from a dataset combining drift and compensation events, to predict, on average, slightly higher speeds than achieved during compensation. Honey buzzards did experience relatively strong absolute crosswinds in spring, suggesting they regularly compensated for wind drift when travelling toward Gibraltar. This example shows it is important to consider that we calculated tail- and crosswind components relative to the realized hourly and daily travel directions, rather than the intended travel direction (Shamoun-Baranes et al. 2007, Nathan et al. 2008, Klaassen et al. 2011, Kemp et al. 2012). We thus studied the influence of wind on flight after they decided how to compensate for side winds and, therefore, wind compensation decisions may account for small seasonal differences in regional behavior (Shamoun-Baranes et al. 2007, Nathan et al. 2008, Klaassen et al. 2011, Kemp et al. 2012).

Daily patterns of hourly behavior

We showed that weather predicted travel performance much less accurately during morning and evening hours compared to mid-day flights, especially for honey buzzards. During the course of a day, the internal motivation and navigational decisions of a soaring migrant may change for reasons other than weather conditions. For example, birds are likely to begin searching for a suitable roosting site in the evening (Tsovel and Allon 1991, Alpert et al. 2000). Moreover, we suspect honey buzzards also react differently to weather in the morning because they are not able to compensate for wind as efficiently as compared to mid-day. This is because, at mid-day, honey buzzards should climb faster in stronger or closely spaced thermals allowing them to exit thermals at higher altitudes (Kerlinger 1989, Bruderer et al. 1994, Spaar and Bruderer 1997a, Shamoun-Baranes et al. 2003c) and to glide more steeply between thermals which are likely to be available along the best possible travel direction to compensate for drift (Pennycuik 2003). Montagu's harriers do not alter their behavior so strongly at specific times of the day, because their superior flapping abilities allow them to move independently of diurnal cycles in the atmosphere (Spaar and Bruderer 1997b).

Negotiating dust-storms

Several honey buzzards made obvious detours over the Sahara and these occurred most frequently in spring. We know some of these detours were caused by dust-storms (Treep 2012), and given the prevalence of detours is higher in spring when dust-storms are most frequent (Goudie and

Middleton 2001), we suspect more detours to be associated to such storms (Strandberg et al. 2010). Our models did not predict flight performance any worse during detours than when keeping course, probably because they were drifting with the wind ahead of a storm, although detours did cause an estimated delay of arrival in Gibraltar of two to six days (Treep 2012). Our tracking data suggests that honey buzzards prefer making a detour, potentially increasing their migration route by several hundred kilometers, rather than to sit and wait through a dust-storm or try and fly through one, a behavior more often observed in ospreys, marsh and Montagu's harriers (R. Strandberg pers. comm. (Lund Univ., Sweden), RHGK and BJK unpubl.). The latter strategies may pose an increased risk of running severe delays, or death by starvation or dehydration (Strandberg et al. 2010, Klaassen et al. 2014), especially during dust-storms that last several days. Considering that we only study migrations that were successfully completed by adult birds returning to the breeding grounds, we should expect these individuals to be well adapted to cope with disadvantageous or dangerous weather.

Implications for migration phenology

While the general timing of migration may in part be endogenously controlled in response to day length (Gwinner and Helm 2003, Visser et al. 2010), general climatic conditions also influence timing of migration (Shamoun-Baranes et al. 2010). For example, long-distance migrating raptors, including both our study species, have advanced their autumn migration passage dates in southern France by 5–10 d over the past 40 yr, probably due to climate change (Filippi-Codaccioni et al. 2010). On an even finer time scale, the onset of migration can be triggered by weather conditions at the region of departure (Shamoun-Baranes et al. 2006, Jaffré et al. 2013). Our results suggest that soaring migrants may also have advanced arrival dates if gradually ameliorating flight conditions have improved migration performance (Gordo 2007).

For example, an increase of 1 m s^{-1} in average tailwind components experienced by a soaring migrant would lead to an increase of 15–20 km travel distance per day. Honey buzzards, which normally travel approx. 160 km per travel day, would then be able to complete their whole journey 2–3 d faster than they do now. Furthermore, higher temperatures would also lead to stronger convection, increased boundary layer height, and thus a higher travel performance (Shamoun-Baranes et al. 2003a, Gordo et al. 2013). Interestingly, conditions for soaring raptors have ameliorated in recent decades over Europe in spring (i.e. higher temperatures and increasing frequency of tailwinds, Hüppop and Hüppop 2003, Pirazzoli and Tomasin 2003, Tøttrup et al. 2008, Kemp et al. 2010) but may, for example, have deteriorated over the Sahara by an increase in the frequency and intensity of dust-storms or crosswinds.

Understanding the impact of migration events within the annual cycle, and subsequent fitness consequences, will require researchers to unravel trends in adverse and supportive weather conditions along entire flyways (Shamoun-Baranes et al. 2010, Gordo et al. 2013, Drake et al. 2014). We also need to separate the effects of weather on migration

performance (including time-consuming detours) from the effects of weather on departure and stop-over decisions in relation to precipitation, wind conditions and foraging opportunities (Meyer et al. 2000, Thorup et al. 2006, Klaassen et al. 2008). We expect interspecific comparisons of behavior such as the analysis presented here will be helpful to further our understanding of the role of weather in shaping the evolution of bird migration (Gordo 2007, Shamoun-Baranes et al. 2010, Gordo et al. 2013, Jaffré et al. 2013).

Conclusions

Soaring migrants use atmospheric currents to travel across the landscape, and their performance is dictated by weather conditions encountered on their way. Our results demonstrate that two soaring migrants were affected similarly by weather conditions across their entire migratory ranges, indicating their flight behavior remained consistent across the full journey. In effect, regional and seasonal weather conditions dictated performance patterns for each species (Tøttrup et al. 2008, Kemp et al. 2010). After accounting for effects of weather, a small but significant effect of regions and seasons on flight performance remained, indicating that soaring migrants do change their flight behavior between regions and seasons. However, the effect on migratory performance is notably small compared to the dominating effects of regional and seasonal variation in weather. More work is needed to determine the effects of weather on other aspects of soaring migration, such as foraging and take-off decisions (Thorup et al. 2006, Klaassen et al. 2008) and strategies for dealing with crosswinds (Klaassen et al. 2011, Bohrer et al. 2012), which ultimately also affect migration performance and timing (Gordo 2007, Nathan et al. 2008, Shamoun-Baranes et al. 2010).

The future analysis of high-resolution migration tracks and behavior inferred from accelerometer data, such as can be obtained with the remotely reprogrammable GPS-loggers we used in this study (Bouten et al. 2013), will allow researchers to further resolve the influence of environmental cues on movement by distinguishing between distinct behavioral responses to the environment (e.g. drift vs compensation, foraging vs resting, flapping vs soaring flight) that are important to interpret performance at multiple scales (Nathan et al. 2008, Shamoun-Baranes et al. 2010).

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Supplementary material (Appendix JAV-00457 at <www.avianbiology.org/readers/appendix>). Appendix 1.